Ann. Natal Mus. Vol. 23(1) Pages 129–144 Pietermaritzburg October, 1977

# The Fresh-water Mollusca of Tongaland, with a note on Molluscan Distribution in Lake Sibaya

by

**C. C. Appleton**

(Bilharzia Field Research Unit, South African Medical Research Council, Nelspruit)

SYNOPSIS

Records of 31 species of fresh-water Mollusca (20 Gastropoda and 11 Lamellibranchiata) from Tongaland are collated. Attention is drawn to the differences between the aquatic malacofaunae of the Pongola River floodplain in the west and the coastal lake systems in the east. Only 10 species (9 Gastropoda and 1 Lamellibranch) are common to both environments. It is suggested that the relationship between *Caelatura framesi* and *C. mossambicensis* (Unionidae) should be investigated. Brief descriptions of some waterbodies are included.

A comparison is made between the vertical distribution of Mollusca in submerged weed beds in sheltered and exposed situations in Lake Sibaya. In the former situation *Biomphalaria pfeifferi* (intermediate host of *Schistosoma mansoni*) was most abundant at 1,4 m but extended to 4,5 m. *Bulinus* (*Physopsis*) *globosus* (intermediate host of *S. haematobium* and *S. mattheei*) did not extend beyond 1,4 m at which depth it was also most abundant. In the latter situation *B. pfeifferi* was found to 0,4 m and *B.*(*Ph.*)*globosus* to 0,3 m.

The diversity of Mollusca in detached waterbodies adjacent to Lake Sibaya decreased with increasing distance from the present lake shore. *B.*(*Ph.*)*globosus* has however spread into much of the peripheral grassland recently inundated by a rise in lake level.

## INTRODUCTION

The distributions of many organisms of tropical origin extend southwards on the low-lying coastal peneplain of south-eastern Africa and the transition from a tropical to a temperate biota becomes apparent in north-eastern Natal (Tongaland). This has been discussed for terrestrial Mollusca by Van Bruggen (1967, 1969) and Van Bruggen & Appleton (in press) and for the fresh-water Mollusca by Brown (1967).

Knowledge of the composition and distribution of the fresh-water component of this malacofauna is however incomplete. The present paper reviews existing records and those of the author's own survey, which included investigations into the vertical distribution of molluscs in Lake Sibaya and its adjacent waterbodies. This synopsis includes records by Kuiper (1966) and Pretorius *et al.* (1975) from the Pongola River floodplain; Allanson *et al.* (1974), Boltt (1969) and Bruton (unpubl. SCUBA diving log data) from Lake Sibaya; Bruton & Appleton (1975) from the Mgobezeleni lake system and Brown (1966, 1967), Brown & Van Eeden (1969), Brown *et al.* (1971*a* & *b*) and Conolly (1939) from Tongaland in general. The author's survey was made in 1973 to assess on a presence/absence basis the distribution of the bilharziasis snail intermediate hosts *Biomphalaria pfeifferi* and *Bulinus* (*Physopsis*) *globosus* in the coastal lake systems of eastern Tongaland. Where possible, localities were visited in both summer and winter. Only in certain habitats in and around Lake Sibaya were quantitative samples taken.

Material collected during a visit to the Pongola River floodplain in April 1973 fills many of the gaps in the species distributions given by Pretorius *et al.* (1975) and endorses their conclusion that qualitatively the aquatic malacofauna of the

floodplain pans does not vary much. These pans are therefore not named individually in the systematic list.

Records of estuarine Mollusca from the saline parts of the Kosi lake system have been given by Boltt & Allanson (1975) and Broekhuysen & Taylor (1959) and from the Mgobezeleni estuary by Bruton & Appleton (1975) and MacNae (1963). These are not considered further here.

## THE COLLECTION AREA AND ITS AQUATIC ENVIRONMENTS

Tongaland, the extreme north-eastern corner of Natal, is considered here to be the area of approximately 900 km² bounded in the north by the Natal/Mozambique border, in the west by the Lebombo Mountain range, in the south by the Mkuzi River and Lake St. Lucia and in the east by the Indian Ocean, i.e. between approximately 26°52′–27°40′S and 32°07′–32°55′W (Fig. 1). It consists predominantly of a sandy coastal plain seldom rising above an altitude of 107 m, and continuous with that of southern Mozambique. The topography rises in the west where the Lebombo Mountains reach an altitude of 604 m.

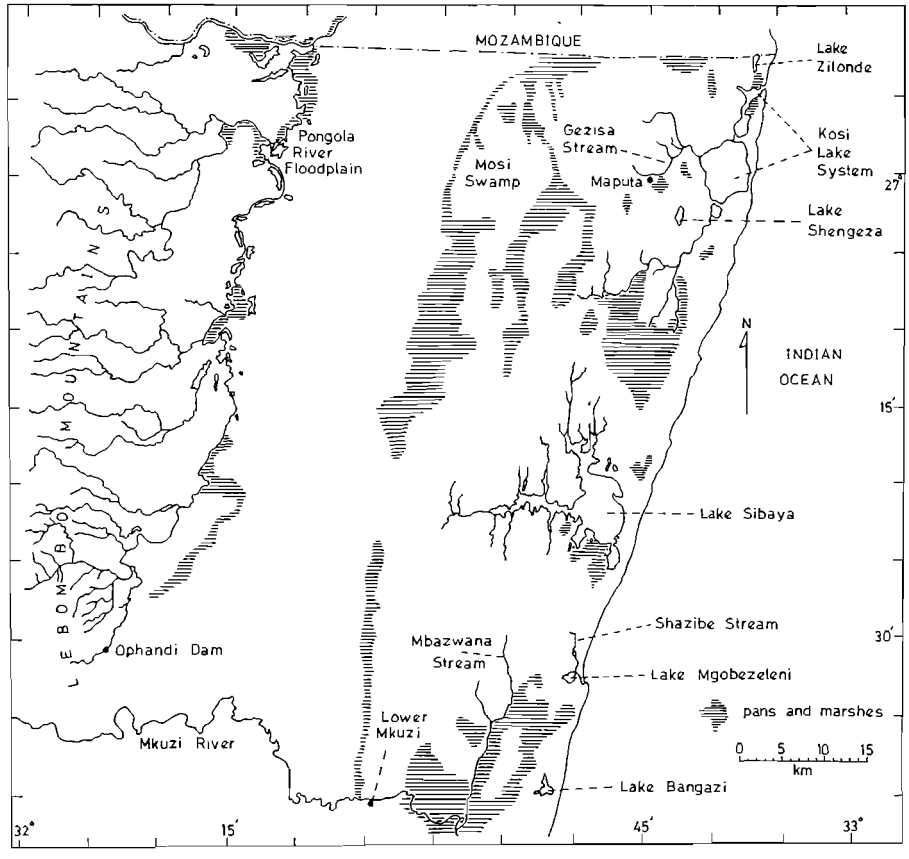


Fig. 1. Map of Tongaland (north-eastern Natal) showing the main localities mentioned in the text.

A regression of the sea during late Pliocene times exposed the marine sediments of the present low-lying coastal peneplain of south-east Africa (King 1972). Coupled with high-water levels due to increased rainfall during the subsequent Pleistocene period (Cooke 1964), this provided a route by which elements of the tropical Mozambique fauna penetrated southwards.

According to the Köppen climatic classification the plain experiences a tropical savanna type of climate with summer rainfall and according to the Thornthwaite scheme, a sub-humid warm climate with sufficient moisture in all seasons (Schulze 1947). Mean annual rainfall decreases westwards from the coast, from 1 130 mm (6 years) at Lake Sibaya Research Station (27°23'S; 32°43'E) in the east to 589 mm (7 years) at Makatini Research Station (27°24'S; 32°11'E) in the west (i.e. approximately 10,2 mm/km), but this increases again over the Lebombo Mountains.

On the basis of the types of waterbody present, Tongaland may be divided into three parts corresponding to the three ecological areas delineated by Van Bruggen (1967); the eastern or coastal, central and western parts. The eastern part is characterized by a series of brackish or fresh-water lakes fed by low-gradient streams and with adjacent smaller waterbodies (ponds and pans). Only the lakes of the Kosi system and Lake Mgobezeleni have open estuaries. The central part is semi-arid in character although it does contain the extensive Mosi swamp running in a north–south direction but much of which is seasonal. The western part includes the Pongola River and its floodplain comprising a series of large pans on either bank. Most of these are perennial and less than 1,5 m deep (Coke & Mc. C. Pott 1971). This floodplain lies between 31 and 46 m altitude, at the foot of and parallel to the Lebombo range. Ophandi dam (27°30'S; 32°25'E) lies in the Lebombo foothills, and is built across the southernmost tributary to the Pongola River.

## AQUATIC HABITATS OF THE EASTERN PART

Locality names have, where possible, followed Tinley (1958) and the 1 : 50 000 trigonometrical survey maps of the area issued by the Government Printer. All waterbodies visited were fresh with electrical conductivities between 135 and 800 $\mu$S.

Lakes Shengeza (27°02'S; 32°47'E) and Zilonde (26°52'S; 32°52'E) are small and windswept with few sheltered habitats. Depths in the two waterbodies reach 6 and 4 m respectively. Transparency is poor, with Secchi disc readings at 1,0 m in Shengeza and 0,63 m in Zilonde. Marginal vegetation is predominantly of *Scirpus litoralis* Schrad., *Rhyncospora glauca* Vahl and *Phragmites* sp. with scattered *Typha latifolia* L., *Nymphoides indica* (L.) Kuntze and *Nymphaea* sp. Submerged beds of *Potamogeton schweinfurthii* A. Benn occur close inshore in Lake Zilonde.

Descriptions of Lake Sibaya have been given by Allanson & Van Wyk (1969) and Allanson *et al.* (1974) and the Mgobezeleni lake system by Bruton & Appleton (1975). In Lake Sibaya much research has been done using SCUBA and the vertical distributions of many molluscs can be reliably quoted.

Waterbodies associated with and adjacent to Lake Sibaya are categorized as ponds, pans and streams. Ponds, the 'lesser lakes' of Tinley (1958), are up to 4 m deep, perennial and open with marginal vegetation. This is mostly *S. litoralis* and *T. latifolia* while submerged macrophytes include *Ceratophyllum demersum* L., *Myriophyllum*

*spicatum* L., *Potamogeton schweinfurthii* and *Nymphaea capensis* Thunb. Secchi disc readings were at 1,9 m in Tsheliwane, 1,2 m in Empayeni and 0,45 m in Matigane.

Pans are shallower (depths may reach 2 m in summer) than ponds and some are seasonal. These are quite different from the pans of the Pongola floodplain which are larger and never filled with emergent vegetation. They are filled with reeds, mostly *S. litoralis*, with only a small, open area in the middle usually containing *N. capensis* and *Utricularia* sp. Vasa pan (27°11'S; 32°46'E) lies just north of Lake Sibaya and may be connected to the Kosi system after heavy rains.

Streams, most of which are perennial, are similar throughout Tongaland. They are pooling watercourses less than 1 m deep and with very low gradients (0,01–0,05%). Measurements with an Ott current meter in Mseleni and Welandhlovu streams (flowing into Lake Sibaya) indicate a mean velocity of approximately 0,13 m/sec though this may reach 0,33 m/sec in summer (Bruton, unpubl. data). Marginal areas are often calm and flanking vegetation is mostly of sedges.

Localities and vertical distribution of 32 species are given where known, in the systematic list. Identifications have been confirmed by taxonomists. Families of Gastropoda and Lamellibranchiata are arranged according to Taylor & Sohl (1962) and Thiele (1935) respectively. The semi-aquatic Succineidae have been omitted since they will be dealt with by Van Bruggen & Appleton (in prep.).

## SYSTEMATIC LIST

Species marked with an asterisk are considered of tropical origin

### Gastropoda

### Prosobranchia

#### Viviparidae

*Bellamya capillata* (Frauenfeld, 1865)*

Pongola River floodplain (Brown 1967; Pretorius *et al.* 1975; present survey); Lake Sibaya (Connolly 1939; Boltt 1969; Allanson *et al.* 1974); Sibaya ponds. A common species found from approx. 0,4 m (Empayeni pond) to 30,4 m on hard sand covered with a 1–2 cm layer of soft detritus in Lake Sibaya (Bruton, unpubl. data).

#### Ampulariidae

*Lanistes ovum* Troschel, 1845*

Pongola River (Connolly 1939), Pongola River floodplain (Brown 1967; Pretorius *et al.* 1975; present survey) common on soft, marginal mud.

#### Thiaridae

*Cleopatra ferruginea* (Lea, 1850)*

Otolini district (Connolly 1939; this may be a mis-spelling of Otobotini); Pongola River floodplain (Brown 1967; Pretorius *et al.* 1975; present survey). Found commonly at approx. 0,5 m amongst marginal vegetation.

*Melanoides tuberculata* Müller, 1874*

Pongola River floodplain (Pretorius *et al.* 1975; present survey); Lake Sibaya (Boltt 1969; Allanson *et al.* 1974); Lake Mgobezeleni (Bruton & Appleton 1975); Lake Shengeza; Gezisa stream; Vasa pan; Mkuzi River at Lower Mkuzi; Sibaya streams; Sibaya ponds. Found in a variety of habitats, from approx. 0,2 m in very shallow streams to 35 m in Lake Sibaya (Boltt 1969). Trichopteran cases (Leptoceridae) were found attached to shells of live snails in Empayeni pond.

Pulmonata

Lymnaeidae

*Lymnaea natalensis* Krauss, 1848.

Pongola River floodplain (Pretorius *et al.* 1975; present survey) Lake Sibaya (Allanson *et al.* 1974); Lake Mgobezeleni and its outflow (Bruton & Appleton 1975); Lake Shengeza; Gezisa stream; Mbazwana stream; Sibaya streams; Shazibe stream; Vasa pan; Sibaya ponds; Sibaya pans. Found amongst marginal vegetation and to 4,7 m on *M. spicatum* in Guguswana Bay (Lake Sibaya).

*Lymnaea columella* Say, 1817.

Pongola River floodplain (Pretorius *et al.* 1975); Ophandi dam and on mangrove trunks in Mgobezeleni estuary (Bruton & Appleton 1975). An exotic species from North America, a recent immigrant to Tongaland.

Ancylidae

*Burnupia* sp.

Lake Sibaya (Allanson *et al.* 1974); Lake Mgobezeleni (Bruton & Appleton 1975); Lake Zilonde; Sibaya ponds; Sibaya pans; Sibaya streams; Mbazwana stream; Ophandi dam.
Records of *Ancylus* sp. (Boltt 1969) obviously refer to this species. Found on marginal vegetation to 4,7 m in submerged weed beds in Lake Sibaya.

*Ferrissia? cawstoni* Walker, 1923.

Pongola River floodplain (Pretorius *et al.* 1975).

*Ferrissia* sp.

Pongola River floodplain; small pan near Bhanga nek; Sibaya ponds; Sibaya pans; Mbazwana stream; Shazibe stream; Lake Mgobezeleni outflow (Bruton & Appleton 1975). Found on emergent vegetation in shallow water.

Planorbidae

*Biomphalaria pfeifferi* (Krauss, 1848)*

Pongola River floodplain (Pretorius *et al.* 1975; present survey); Lake Sibaya (Allanson *et al.* 1974); Lake Mgobezeleni (Bruton & Appleton 1975); Gezisa stream at Maputa; Sibaya ponds; Ophandi dam. Found on marginal vegetation to 4,5 m on *M. spicatum* in Guguswana Bay (Lake Sibaya) and to 1,6 m on *S. litoralis* and firm sandy mud in Empayeni pond.

*Gyraulus costulatus* Krauss, 1848*

Tongaland (Brown & Van Eeden 1968); Pongola River floodplain (Pretorius *et al.* 1975; present survey); Lake Sibaya (Allanson *et al.* 1974); Lake Mgobezeleni (Bruton & Appleton 1975); Sibaya ponds; Mkuzi River at Lower Mkuzi; Mbazwana stream; Sibaya streams. Found on marginal vegetation to 1,8 m on submerged *M. spicatum* (Lake Sibaya).

Small planorbid Gastropoda previously classified as *Anisus natalensis* (Krauss, 1848) and *A. coretus* (De Blainville, 1826) have been placed in two new genera, *Ceratophallus* and *Afrogyrus* by Brown & Mandahl-Barth (1973).

*Ceratophallus* sp.

Lake Mgobezeleni and its outflow (Bruton & Appleton 1975); Lake Sibaya; Sibaya ponds; Sibaya pans; Shazibe stream.

Dr D. S. Brown writes of these specimens (14/3/74), 'It seems necessary to be inconclusive as in none of your lots did I find a snail with the penis fully sclerotized as in *C. natalensis*. Possibly this is because all your specimens are immature, but I doubt it and feel that there is an undescribed species in Natal and Mozambique that is characterized by its small size and short copulatory organ, with slightly sclerotized penis.' Found on marginal vegetation and submerged weed to 6 m (in a submerged *M. spicatum* bed in main basin of Lake Sibaya). Two scalariform freaks were collected amongst emergent *T. latifolia* at 0,4 m in Empayeni pond.

*Afrogyrus coretus* (De Blainville, 1826)*

Lake Mgobezeleni (Brown 1967); Mhlongeni pan on sedges in shallow water.

*Segmentorbis angustus* (Jickeli, 1874)*

Lake Mgobezeleni outflow (Bruton & Appleton 1975); Lake Zilonde; Shazibe stream. Found on marginal vegetation in sheltered habitats.

*Segmentorbis kanisaensis* (Preston, 1914)*

Lake Mgobezeleni (Brown 1967); Lake Mgobezeleni outflow (Bruton & Appleton 1975); Lake Zilonde; Shazibe stream. Found in similar situations to the above.

*Lentorbis junodi* (Connolly, 1925)*

Pongola River floodplain; Lake Mgobezeleni outflow (Bruton & Appleton 1975); Lake Zilonde; Sibaya pans; Shazibe stream. Found in similar situations to *S. angustus*.

*Bulinus* (*Bulinus*) *natalensis* (Kuster, 1841)*

Pongola River floodplain (Brown *et al.* 1971; Pretorius *et al.* 1975; present survey); Lake Sibaya (Connolly 1939; Boltt 1969; Brown *et al.* 1971; Allanson *et al.* 1974); Lake Mgobezeleni and its outflow (Bruton & Appleton 1975); Lake Umpangazi (probably Lake Bangazi, 27°37'S; 32°24'E) and Mozi pan, the perennial southern end of the Mozi swamp, 27°39'S; 32°38'E (Brown *et al.* 1971); Lake Zilonde; Lake Shengeza; Sibaya ponds. Found on marginal and submerged vegetation to 7 m in Lake Sibaya (Boltt 1969).

Quantitative sampling in Empayeni pond (adjacent to Lake Sibaya) revealed that *B. natalensis* has only one generation per year, unlike other local planorbids which have three (Appleton 1974). *Bulinus natalensis* which takes six months to reach maturity is thus a slow-growing species, a feature which seems compatible with the suggestion by Brown *et al.* (1971*b*) that on morphological grounds it is adapted to lacustrine (i.e. stable) conditions.

*Bulinus* (*Bulinus*) *tropicus* (Krauss, 1848)

Mkuzi River at Lower Mkuzi.

Brown *et al.* (1971*a* & *b*) concluded that in south-eastern Africa *B. natalensis* and *B. tropicus* are difficult to separate reliably on account of continuous variation among recognized characteristics, perhaps due to interbreeding. Most populations in Tongaland however correspond to nominal *B. natalensis* and are considered as such by the above authors.

*Bulinus* (*Bulinus*) *forskali* (Ehrenberg, 1831)*

Pongola River floodplain (Pretorius *et al.* 1975; present survey). Found on firm mud, shallow submerged and marginal vegetation.

*Bulinus* (*Physopsis*) *globosus* (Morelet, 1866)*

Pongola River floodplain (Brown 1966); Lake Mgobezeleni outflow (Bruton & Appleton 1975); Gezisa stream; Mbazwana stream; Vasa pan; Sibaya ponds; Sibaya pans. Found on marginal vegetation and to about 2,0 m on *S. litoralis* and submerged *M. spicatum*, and to 0,3 m on sheltered sand in which it was noted to bury itself. A large specimen (9,5 × 6,7 mm) was found being attacked by a 19 mm larva of *Luciola* sp. (Coleoptera: Lampyridae), and a small leech, *Batracobdella tricarinata* Blanchard, was taken from the mantle cavity of a juvenile snail. Dr J. H. Oosthuizen mentions (in litt. 30/1/73) that this occurs commonly amongst leeches such as this, belonging to the Glossiphoniidae.

Pretorius *et al.* (1975) and Allanson *et al.* (1974) have recorded *Bulinus* (*Physopsis*) *africanus* (Krauss, 1848) from the Pongola floodplain and Lake Sibaya respectively, but there remains uncertainty over these identifications and indeed over the very validity of two species within the subgenus *Bulinus* (*Physopsis*) in South Africa, viz. *africanus* and *globosus* (Dr G. Oberholzer, pers. comm.) Brown (1966) concluded that only *B.* (*Ph.*) *globosus* occurred on the north-eastern coastal plain of Natal.

Lamellibranchiata

Eulamellibranchiata

Unionidae

*Caelatura framesi* (Connolly, 1925)*

Pongola River floodplain (Brown 1967; present survey).

This species, recorded by Connolly (1939) as *Unio framesi*, belongs in the genus *Caelatura* and although Brown (1967) referred to it as such, he gave no reasons for doing so. This is a valid change however since the Pongola specimens (and those from the Komati River, eastern Transvaal) possess important characteristics of

*Caelatura*, namely the modification of the major part of all four gill lamellae to serve as marsupia, zigzag sculpture extending posteriorly, anteriorly and sometimes medially and a markedly raised postero-dorsal margin giving the shell a triangular shape. In *Unio* only the outer lamellae are modified to function as marsupia, zigzag sculpture is confined to the umbonal area and visible only in juveniles and the general shell shape is elliptical (Thiele 1935).

*Caelatura framesi* is the common and indeed the only unionid on the Pongola River floodplain (Prof. J. Heeg, in litt., 25/11/76) and the *Unio mossambicensis* (Martens, 1859) recorded from the floodplain by Pretorius *et al.* (1975) presumably refers to this species. Martens' species is known from the Zambezi River system (Connolly 1939; Haas 1936; Marshall 1975) and Lake Malawi northwards (Crowley *et al.* 1964; Mandahl-Barth 1972) and according to the two latter authorities, also belongs in the genus *Caelatura*. Both *framesi* and *mossambicensis* are thin-shelled species with delicate though poorly developed sculpture. Their relationship should be investigated.

Mutelidae

*Aspatharia* (*Spathopsis*) *wahlbergi* (Krauss, 1848)*

Pongola River floodplain (Pretorius *et al.* 1975); Ophandi dam.

*Aspatharia* (*Spathopsis*) *petersi* (Martens, 1859)*

Pongola River floodplain (Pretorius *et al.* 1975).

Cyrenidae

*Corbicula africana* (Krauss, 1848)*

Pongola River floodplain (Pretorius *et al.* 1975; present survey); Lake Sibaya (Boltt 1969; Allanson *et al.* 1974); Sibaya ponds; Mkuzi River at Lower Mkuzi. Found from approx. 0,5 m in sheltered sand to 33 m in silt substrate in Lake Sibaya (Boltt 1969).

Sphaeriidae

*Sphaerium capense* (Krauss, 1848)*

Lake Sibaya (Allanson *et al.* 1974); Lake Mgobezeleni (Bruton & Appleton 1975); Lake Zilonde; Sibaya ponds; Gezisa stream; Shazibe stream. Found in sandy and muddy substrata, to about 2,9 m in Lake Zilonde, 1,1 m in Tsheliwane, 1,5 m in south-west basin of Lake Sibaya.

*Sphaerium incomitatum* (Kuiper, 1966)*

Lake Mgobezeleni (Bruton & Appleton 1975); Lake Zilonde; Mbazwana stream. Found in situations similar to above. These are the only known occurrences of this species in the Republic of South Africa. The umbonal area is frequently covered by a ferruginous incrustation. Dr J. Kuiper (in litt. 9/2/75) notes that the Lake Zilonde specimens, of which the largest measures 8,60 × 6,95 × 4,30 mm, are considerably larger than the type series from Lake MacIlwaine, Rhodesia.

*Sphaerium capense* and *S. incomitatum* were found together in Lakes Mgobezeleni (Bruton & Appleton 1975) and Zilonde (present survey). Further collecting in

Sibaya and other coastal lakes may show these two species to be sympatric over this part of the coastal plain. They may readily be distinguished by the curvature of the anterior margin of the shell as well as the position and shape of the umbone. In *S. capense* the anterior margin is rounded whereas in *S. incomitatum* it is more pointed. The umbone of *S. capense* is broader and situated anterior to the vertical median line while in *S. incomitatum* it is more rounded and lies posterior to the line.

*Pisidium langleyanum* Melvill & Ponsonby, 1891

Mbazwana stream, in shallow sand amongst marginal vegetation.

*Pisidium ovampicum* Ancey, 1890

Lake Mgobezeleni outflow (Bruton & Appleton 1975); Shazibe stream; Gezisa stream. Found in shallow sand.

*Pisidium pirothi* Jickeli, 1881*

Pongola River floodplain (Kuiper 1966; Brown 1967; Pretorius *et al.* 1975).

*Eupera ferruginea* (Krauss, 1848)*

Pongola River floodplain (Pretorius *et al.* 1975); Lake Sibaya (Allanson *et al.* 1974) at approx. 2,7 m in a sheltered bay, possibly attached to *M. spicatum* plants.

*Eupera parasitica* (Deshayes, 1854)*

Pongola River floodplain (Brown 1967; present survey). Found in shallow mud amongst marginal vegetation.

## DISTRIBUTION IN LAKE SIBAYA

In Lake Sibaya Boltt (1969) has shown that *Bellamya capillata* and *Melanoides tuberculata* are amongst the most abundant invertebrates on sand and silt substrates in the main basin, being distributed from shallow terraces (0–2 m) to beyond the 24 m depth contour. *Corbicula africana* was recorded to 33 m while *Bulinus natalensis* occurred in both weed and sand to the limit of the submerged weed belt at approximately 7 m.

Submerged weed beds in sheltered, eutrophic bays (along all except the lake's eastern shore) harbour a rich aquatic malacofauna. Twelve species were recorded by Allanson *et al.* (1974) whereas Boltt (1969) had found only five in similar beds in exposed situations in the main basin. In order to compare the vertical distribution of molluscs in a sheltered bed with another in an exposed situation, series of samples were taken in May and July 1973 over two beds, one protected and the other exposed.

The sheltered bed was in Guguswana Bay in the lake's south basin, where a dense fringe of the reeds *Scirpus litoralis*, *Typha latifolia* and the herb *Polygonum tomentosum*, dominated the marginal vegetation. *Nympaea capensis* and an extensive submerged bed of *Ceratophyllum demersum*, *Myriophyllum spicatum* and *Potamogeton schweinfurthii* occurred in the open water beyond. The other bed, off the exposed southern shore of the south basin, comprised *S. litoralis*, *C. demersum* and *M. spicatum*.

Qualitative weed samples were taken by diving at approximately 5 m intervals from the marginal vegetation along transect lines over the beds. The results are

presented in Figure 2. The Guguswana samples from 0,5 to 5,0 m, expressed quantitatively as the number of snails per kilogram wet weight of weed (mostly *M. spicatum*), are given for seven species in Table 1.

TABLE 1

*Guguswana Bay transect: results expressed as no. snails per kilogram of weed (wet weight)*

| Depth (m) | *M. tuberculata* | *L. natalensis* | *Burnupia* sp. | *B. pfeifferi* | *Cerato-phallus* sp. | *Bulinus natalensis* | *Bulinus (Physopsis) globosus* |
|---|---|---|---|---|---|---|---|
| 0,5 . . | 1,4 | 1,1 | 0 | 5,0 | 0 | 3,6 | 1,8 |
| 1,0 . . | 3,0 | 0,7 | 0,3 | 4,0 | 0,3 | 7,3 | 1,6 |
| 1,4 . . | 4,9 | 6,4 | 0 | 7,7 | 0,5 | 21,0 | 2,3 |
| 2,8 . . | 7,9 | 1,8 | 2,3 | 3,3 | 0,7 | 43,9 | 0 |
| 3,2 . . | 13,2 | 0 | 1,1 | 1,2 | 0,7 | 29,6 | 0 |
| 4,3 . . | 3,6 | 0 | 0 | 1,1 | 0 | 10,7 | 0 |
| 3,7 . . | 4,0 | 0,5 | 0,5 | 1,0 | 0 | 16,0 | 0 |
| 4,5 . . | 3,9 | 0,3 | 0,7 | 2,8 | 0 | 26,7 | 0 |
| 4,7 . . | 1,4 | 0 | 0,7 | 0 | 0 | 17,5 | 0 |
| 5,0 . . | 6,7 | 0 | 0 | 0 | 0 | 6,0 | 0 |

It is evident that in the sheltered weed bed pulmonates (except *B. natalensis* and *Burnupia* sp.) penetrate deeper than in the exposed one which experiences considerable wave action. The presence in the Guguswana samples of several lymnaeid egg-capsules attached to weed at depths from 1,0 to 4,7 m indicates that *L. natalensis* (the only lymnaeid present) breeds well below the surface. Likewise the finding of juvenile (maximum shell dimension 1,0–1,5 mm) *B. pfeifferi*, *B. natalensis* and *Burnupia* sp. at 4,5, 5,0 and 4,5 m respectively suggests that they might do so as well. Table 1 shows that the six Pulmonata sampled here were most abundant between 1,4 and 2,8 m at the time of the investigation (July 1973). It is clear that these snails, particularly *B. pfeifferi*, hitherto regarded as inhabitants of marginal waters less than about 2 m deep (WHO, 1957), can successfully colonize habitats to several times this depth.

Further, since weed fronds do not reach the surface these snails must obtain their oxygen directly from the water, utilizing cutaneous respiration alone. Experiments by Deschiens & Jardin (1954), Gillet *et al.* (1960) and Alberts (1966) suggest that members of the pulmonate genera, *Biomphalaria*, *Bulinus* and *Lymnaea*, are capable of surviving for prolonged periods without access to a water/air interface. In the micro-climate of these protected weed beds temperatures are stable, seldom rising above 25,5°C or varying by more than 2°C each day (Appleton 1976). Also since the dissolved oxygen concentration is likely to remain close to saturation due to photosynthesis (except close to the mud substrate), the necessity for these pulmonates to migrate to the surface for atmospheric oxygen may well be eliminated.

Separation of sheltered bays such as this to form shallow ponds up to 1 km from the lake has occurred over past decades due to a lowering of the lake's water level. Through further drying, these detached though perennial ponds have become the very shallow pans lying up to 4 km from the lake. Thermal regimes become hotter and more variable as this sequence proceeds (Appleton 1976) but the number of

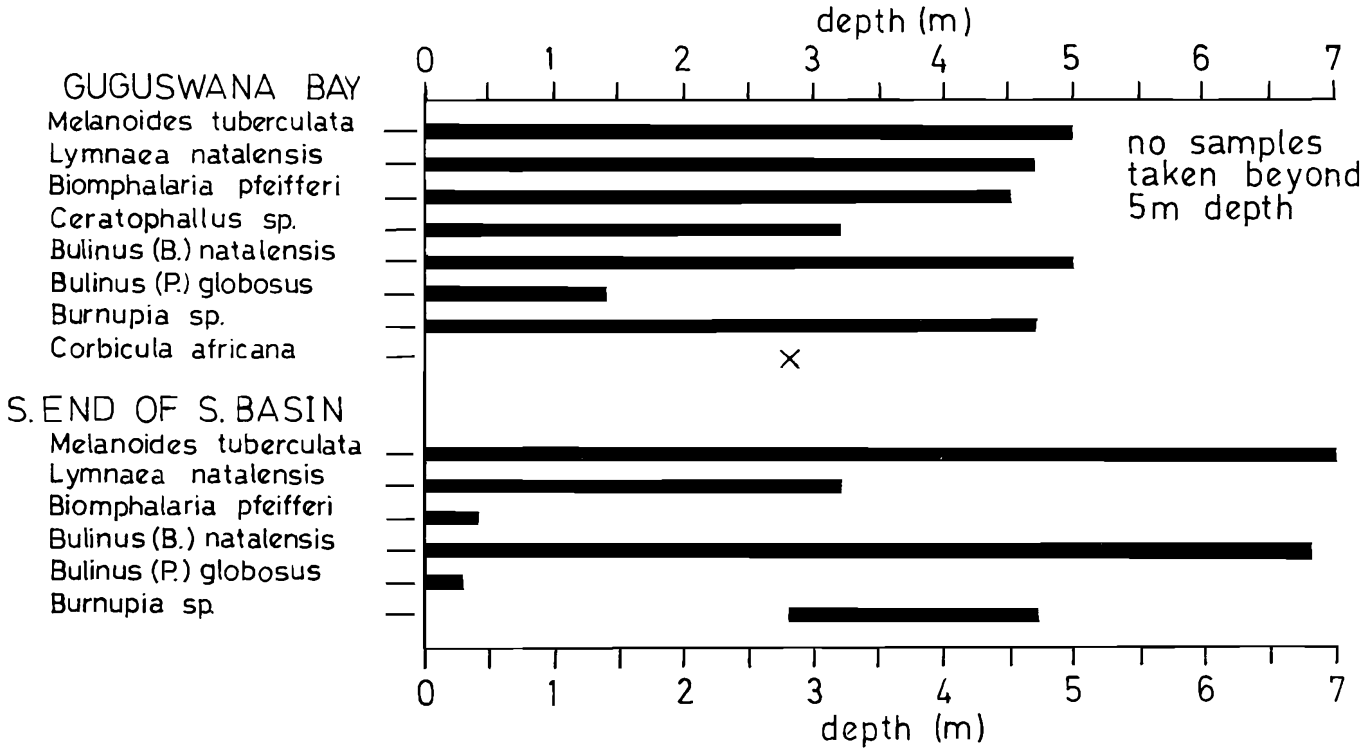


Fig. 2. Diagrammatic representation of the vertical distribution of Mollusca in the sheltered weed bed in Guguswana Bay (south basin, Lake Sibaya) and the exposed bed at the southern end of the south basin.

species present becomes less (Table 2). Thus the degree of affinity between the aquatic malacofaunae of these three habitat types (calculated according to Balinsky 1967) decreases from 90% (between sheltered bays and ponds) to 53% (ponds and pans) to 42% (sheltered bays and pans). The decreasing abundance of the pulmonate *Biomphalaria pfeifferi* in this waterbody sequence was investigated by Appleton (1976), and found to be the result of lowered fecundity due to excessively high temperatures during spring and early summer.

TABLE 2

*The occurrence of fresh-water Mollusca in lentic waterbodies associated with Lake Sibaya*

| Species | Sheltered bays within Lake Sibaya | Perennial waterbodies adjacent to Lake Sibaya | |
|---|---|---|---|
| | | Ponds | Pans |
| Gastropoda | | | |
| *Bellamya capillata* | × | × | |
| *Melanoides tuberculata* | × | × | |
| *Lymnaea natalensis* | × | × | × |
| *Burnupia* sp. | × | × | × |
| *Ferrissia* sp. | | × | × |
| *Biomphalaria pfeifferi* | × | × | |
| *Gyraulus costulatus* | × | × | |
| *Afrogyrus coretus* | | | × |
| *Ceratophallus* sp. | × | × | × |
| *Lentorbis junodi* | | | × |
| *Bulinus (B.) natalensis* | × | × | |
| *Bulinus (Ph.) globosus* | × | × | × |
| Lamellibranchiata | | | |
| *Corbicula africana* | × | × | |
| *Sphaerium capense* | × | × | |
| *Eupera ferruginea* | × | | |

Since the completion of the author's survey, a sustained rise in lake level (2,2 m from 1974 to 1976) has rejoined Empayeni pond and probably others as well to the lake and inundated much low-lying grassland. Pans remained separated though they increased in area and depth. Hydrological data (Pitman & Hutchison 1975) suggests that this inundative phase may be a temporary one, lasting for 2–3 years, to be followed by a lowering of the lake level and presumably separation again of adjacent ponds.

An important result of the inundation of this grassland was its colonization by *Bulinus (Ph.) globosus*—the intermediate host of both (*Schistosoma haematobium* (Bilharz), human urinary bilharzia and *Schistosoma mattheei* Veglia & Le Roux, bovine bilharzia in the area. Previously this snail was known only from the marginal vegetation of all but the barren, oligotrophic shores of the lake. In May 1976 it not only seemed more common in the inundated areas than it had been in the 'old' marginal fringe, but was often the only mollusc found. It appears to be a 'pioneer' species.

## DISCUSSION

This molluscan assemblage is largely a tropical one. The definition of a tropical species used here is that of Stuckenberg (1969), '. . . one which has the greater part of its range within the cartographical tropics', but the assemblage so derived does not

TABLE 3

*Molluscan species known from the Pongola River floodplain on the west of the Tongaland plain and the coastal lake systems on the eastern side*

| Species | Pongola River floodplain | Coastal lake systems |
|---|---|---|
| Gastropoda | | |
| *Lamistes ovum* | × | |
| *Bellamya capillata* | × | × |
| *Cleopatra ferruginea* | × | |
| *Melanoides tuberculata* | × | × |
| *Lymnaea natalensis* | × | × |
| *Lymnaea columella* | × | × |
| *Biomphalaria pfeifferi* | × | × |
| *Gyraulus costulatus* | × | × |
| *Segmentorbis angustus* | | × |
| *Segmentorbis kanisaensis* | | × |
| *Lentorbis junodi* | × | × |
| *Bulinus forskali* | × | |
| *Bulinus natalensis* | × | × |
| *Bulinus (Physopsis) globosus* | × | × |
| Lamellibranchiata | | |
| *Caelatura framesi* | × | |
| *Aspatharia wahlbergi* | × | |
| *Aspatharia petersi* | × | |
| *Corbicula africana* | × | × |
| *Sphaerium capense* | | × |
| *Sphaerium incomitatum* | | × |
| *Eupera ferruginea* | | × |
| *Eupera parasitica* | × | |
| *Pisidium langleyanum* | | × |
| *Pisidium ovampicum* | | × |
| *Pisidium pirothi* | × | |

*Ceratophallus* sp. and *Afrogyrus coretus* are omitted because insufficient material has been critically examined, and *Bulinus* (*Ph.*) *africanus*, *Burnupia* and *Ferrissia*, because of their uncertain taxonomy.

differ from that given by Brown (1967) using the definition of Poynton (1964), '. . . one having at least a substantial part of its range within the area experiencing a tropical climate, i.e. enclosed by the 18°C mean July isotherm'.

Species marked with an asterisk in the systematic list are thus considered tropical and comprise 71,0% (22 species) of the total with one possible addition, *Ceratophallus* sp. Three species (9,7%) *Bulinus tropicus*, *Lymnaea natalensis* and *Pisidium ovampicum* are, as pointed out by Brown (1967), distributed over much of temperate southern Africa and therefore should be excluded from a tropical assemblage. One species considered by Brown to be endemic to South Africa, *Pisidium langleyanum*, has since been reported from Lake Bangweulu (N. Zambia) by Mandahl-Barth (1968). An exotic species, *Lymnaea columella*, was not recorded from Tongaland by Van Eeden & Brown (1966) or Brown (1967) but has since been found on the Pongola floodplain (Pretorius *et al.* 1975) and in the mangrove swamp in the Mgobezeleni estuary (Bruton & Appleton 1975). Brown (1967) has further noted that five of these tropical species (*Lanistes ovum*, *Bellamya capillata*, *Cleopatra ferruginea*, *Caelatura framesi* and *Pisidium pirothi*) reach the southern limits of their ranges in Tongaland, and investigations on the Pongola floodplain (Pretorius *et al.* 1975) in Lake Mgobezeleni (Bruton & Appleton 1975) have revealed two more, *Aspatharia petersi* and *Sphaerium incomitatum*.

The lack of quantitative information on species abundance precludes any meaningful, ecological interpretation of these distribution patterns. It is nevertheless of interest that although 18 species are known from the Pongola River floodplain in the west and 17 from the coastal lake systems in the east, only 10 (40%): 1 lamellibranch and 9 gastropods are common to both environments (Table 3). Species found only on the Pongola floodplain include the operculates *Lanistes ovum* and *Cleopatra ferruginea*, the bulinid *Bulinus forskali* (frequent inhabitants of shallow, muddy habitats) and the large, unionacean mussels *Caelatura framesi*, *Aspatharia wahlbergi* and *A. petersi*. All of these may be expected to tolerate the markedly fluctuating water levels and even periods of dessication that occur here (Coke & Mc. C. Pott. 1971).

Species found predominantly or only in the eastern part where habitats are much more stable include the small pulmonates *Segmentorbis angustus*, *S. kanisaensis*, and the small sphaeriid mussels *Sphaerium capense*, *S. incomitatum*, *Pisidium langleyanum* and *P. ovampicum*.

## SUMMARY

Records of the fresh-water Mollusca from Tongaland are reviewed. Only 40% of species occurring on the Pongola River floodplain in the west are known from the coastal lake systems in the east. This difference may be due to the markedly different environmental conditions in aquatic habitats in the two areas.

Observations made in Lake Sibaya show that several pulmonate snails, including *Biomphalaria pfeifferi* the intermediate host of human intestinal bilharzia, usually regarded as dwellers in marginal vegetation are capable of living to depths of about 5 m in sheltered, submerged weed beds. A decline in the number of species in lentic habitats associated with the lake corresponds to the increasing severity of the habitat's thermal regimes. Following a considerable rise in lake level, the intermediate host of human urinary bilharzia, *Bulinus* (*Ph.*) *globosus*, has spread into extensive areas of inundated grassland.

## ACKNOWLEDGEMENTS

The author is indebted to Dr D. S. Brown (British Medical Research Council), Prof. J. A. van Eeden (Potchefstroom University) and Dr J. G. J. Kuiper (Paris) for identifying the Mollusca and to Dr H. Bertrand (Paris) and Dr J. Oosthuizen (Pretoria University) for identifications of *Luciola* and *B. tricarinata* respectively. The assistance of Mr M. N. Bruton (Officer-in-charge, Lake Sibaya Research Station) in collecting material and of Mr M. Coke (Natal Parks Board) in guiding the author on the Pongola floodplain is also acknowledged. Dr Brown kindly read the manuscript of this paper which is published with the permission of the South African Medical Research Council.

## REFERENCES

ALBERTS, L. E., 1966. Some aspects of the respiratory physiology of three South African fresh-water pulmonate snails, *Bulinus africanus*, *Bulinus tropicus* and *Lymnaea natalensis*. *S. Afr. J. Sci.* **62**: 215–222.

ALLANSON, B. R., BRUTON, M. N. & HART, R. C., 1974. The plants and animals of Lake Sibaya, KwaZulu, South Africa: a check-list. *Rev. Zool. afr.* **88**: 507–532.

ALLANSON, B. R. & VAN WYK, J. D., 1969. An introduction to the physics and chemistry of some lakes in northern Zululand. *Trans. roy. Soc. S. afr.* **38**: 217–240.

APPLETON, C. C., 1974. The population fluctuations of five fresh-water snail species in the eastern Transvaal lowveld, and their relationship to known bilharzia transmission patterns. *S. Afr. J. Sci.* **70**: 145–150.

——— 1976. The influence of abiotic factors on the distribution of *B. pfeifferi* (Krauss, 1848) (Planorbidae: Mollusca) and its life-cycle in south-eastern Africa. Unpublished M.Sc. thesis, Rhodes University. 92 pp.

BALINSKY, B. I., 1967. On some intrinsic and environmental factors controlling the distribution of dragonflies (Odonata), with redescription and a new name for a little known species. *J. Ent. Soc. S. Afr.* **29**: 3–22.

BOLTT, R. E., 1969. The benthos of some southern African lakes. Part II: the epifauna and infauna of Lake Sibaya. *Trans. roy. Soc. S. Afr.* **38**: 249–269.

BOLTT, R. E. & ALLANSON, B. R., 1975. The benthos of some southern African lakes. Part III: the benthic fauna of Lake Nhlange, KwaZulu, South Africa. *Trans. roy. Soc. S. Afr.* **41**: 241–262.

BROEKHUYSEN, G. J. & TAYLOR, H., 1959. The ecology of South African estuaries. Part VIII. Kosi Bay estuary system. *Ann. S. Afr. Mus.* **44**: 279–296.

BROWN, D. S., 1966. On certain morphological features of *Bulinus africanus* and *B. globosus* (Mollusca: Pulmonata) and the distribution of these species in south-eastern Africa. *Ann. Natal Mus.* **18**: 401–415.

——— 1967. A review of the freshwater Mollusca of Natal and their distribution. *Ann. Natal Mus.* **18**: 477–494.

BROWN, D. S. & MANDAHL-BARTH, G., 1973. Two new genera of Planorbidae from Africa and Madagascar. *Proc. malac. Soc. Lond.* **40**: 287–302.

BROWN, D. S., OBERHOLZER, G. & VAN EEDEN, J. A., 1971a. The *Bulinus natalensis/tropicus* complex (Basommatophora: Planorbidae) in south-eastern Africa. I. Shell, mantle, copulatory organ and chromosome number. *Malacologia* **11**: 141–170.

——— 1971b. The *Bulinus natalensis/tropicus* complex (Basommatophora: Planorbidae) in south-eastern Africa: II. Some biological observations, taxonomy and general discussion. *Malacologia* **11**: 171–198.

BROWN, D. S. & VAN EEDEN, J. A., 1969. The molluscan genus *Gyraulus* (Gastropoda: Planorbidae) in southern Africa. *Zool. J. Linn. Soc.* **48**: 305–331.

BRUTON, M. N. & APPLETON, C. C., 1975. Survey of Mgobezeleni lake system in Zululand, with a note on the effect of a bridge on the mangrove swamp. *Trans. roy. Soc. S. Afr.* **41**: 283–294.

COKE, M. & MC. C. POTT, R., 1971. The Pongola floodplain pans. *News Lett. Limnol. Soc. South Afr.* **16**: 20–26.

CONNOLLY, M., 1939. A monographic survey of South African non-marine Mollusca. *Ann. S. Afr. Mus.* **33**: 1–660.

COOKE, H. B. S., 1964. The Pleistocene environment in southern Africa. *Ecological Studies in Southern Africa*, Ed. D. H. S. Davies. The Hague: W. Junk Publishers, 1–23.

CROWLEY, T. E., PAIN, T. & WOODWARD, F. R., 1964. A monographic review of the Mollusca of Lake Nyasa. *Ann. Mus. R. Afr. Centr.*, 8° *Zool.* **131**: 1–58.

DESCHIENS, R. & JARDIN, J., 1954. Viabilité des mollusques vecteurs des bilharzioses dans les eaux profondes. *Bull. Soc. Path. Exot.* **47**: 668–671.

GILLET, J., BRUAUX, P. & WOLFS, J., 1960. Résultats de prospections malacogiques en profondeur au lac Kivu et recherches sur la survie de *Biomphalaria* en eau profonde. *Ann. Soc. Belge de Méd. Trop.* **40**: 643–649.

HAAS, F., 1936. Binnen-mollusken aus Inner-Afrika. *Abh. Senckenbergnaturf. Ges.* **431**: 1–156.

KING, L., 1972. The coastal plain of southeast Africa: its form, deposits and development. *Z. geomorph. N.F.* **16**: 239–251.

KUIPER, J. G. J., 1966. Les espéces africaines du genre *Pisidium*, leur synonymie et leur distribution (Mollusca, Lamellibranchiata, Sphaeridae). *Ann Mus. R. Afr. Centr.*, 8° *Zool.* **151**: 1–78.

MACNAE, W., 1963. Mangrove swamps in South Africa. *J. Ecol.* **51**: 1–25.

MANDAHL-BARTH, G., 1968. Hydrobiological survey of the Lake Bangweulu–Luapula River basin. Freshwater molluscs. *Expl. hydrobiol. Bangweulu–Luapula, scientific results* **12**: 1–96.

——— 1972. The freshwater Mollusca of Lake Malawi. *Rev. Zool. Bot. Afr.* **86**: 257–289.

MARSHALL, B. E., 1975. Observations on the freshwater mussels (Lamellibranchiata: Unionacea) of Lake McIlwaine, Rhodesia. *Arnoldia* **7**: 1–15.

PITMAN, W. V. & HUTCHISON, I. P. G, 1975. *A preliminary hydrological survey of Lake Sibaya.* Report No. 4/75, Hydrological Research Unit, Univ. of the Witwatersrand, Johannesburg. 35 pp.

POYNTON, J. C., 1964. The Amphibia of southern Africa: a faunal study. *Ann. Natal Mus.* **17**: 1–334.

PRETORIUS, S. J., JENNINGS, A. C., COERTZE, D. J. & VAN EEDEN, J. A., 1975. Aspects of the freshwater Mollusca of the Pongola River floodplain pans. *S. Afr. J. Sci.* **71**: 208–212.

SCHULZE, B. R., 1947. The climates of South Africa according to the classifications of Köppen and Thornthwaite. *S. Afr. geogr. J.* **29**: 32–42.

STUCKENBERG, B. R., 1969. Effective temperature as an ecological factor in southern Africa. *Zool. Afr.* **4**: 145–197.

TAYLOR, D. W. & SOHL, N. F., 1962. An outline of gastropod classification. *Malacologia* **1**: 7–32.

THIELE, J., 1935. *Handbuch der systematischen weichtierkunde*, II. Stuttgart: Gustav Fisher. 1154 pp.

TINLEY, K. L., 1958. A preliminary report on the ecology of Lake Sibaya, Tongaland. Natal Parks Board records, unpublished.

VAN BRUGGEN, A. C., 1967. Preliminary note on the distribution of the land molluscs of Tongaland. (N.E. Zululand). *Palaeoecology of Africa.* **2**: 87–90.

——— 1969. Studies on the land molluscs of Zululand with notes on the distribution of land molluscs in southern Africa. *Zool. Verh. Leiden* **103**: 1–116.

VAN EEDEN, J. A. & BROWN, D. S., 1966. Colonization of freshwater in the Republic of South Africa by *Lymnaea columella* Say (Mollusca: Gastropoda). *Nature* **210**: 1172–1173.